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AGE, GROWTH, MORTALITY, FOOD AND REPRODUCTION OF THE SCAMP, MYCTEROPERCA PHENAX, COLLECTED OFF NORTH CAROLINA AND SOUTH CAROLINA

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ABSTRACT

From 1972 to 1979, 7,980 scamp, Mycteroperca phenax, were sampled from South Atlantic Bight fisheries: 3,075 were obtained from the recreational headboat fishery and 4,905 from commercial handline vessels operating out of South Carolina. Biological data were analyzed to determine growth, mortality rates, the reproductive cycle, and diet. Annulus formation on otoliths occurred between December and April. The oldest fish aged was 21 years and measured 893 mm fork length (FL). Back-calculated mean lengths at annulus formation were 216, 336, 415, 470, 515, 552, 584, 613, 639, 663, 686, 707, 726, 746, 769, 791, 820, 833, 873, 883, and 893 mm FL, at ages 1 to 21. The von Bertalanffy equation describing theoretical growth was $l_t = 985(1 - e^{-0.092(t+2.45)})$ where $l_t = FL$ in mm at time t. The length-weight relationship for combined sexes was $W = 2.4 \times 10^{-8} FL^{2.910}$, where W = weight in kg, and FL = fork length in mm. The relationship of total length (TL) to fork length was FL (mm) = 0.870(TL) + 23.625. Annual instantaneous total mortality (Z) estimates ranged from 0.29 to 0.64, for samples from headboats, and from 0.57 to 0.91 for samples from commercial vessels, but the estimates are suspect because of the unusual form of the catch curves. A Beverton and Holt yield-per-recruit model suggests a maximum yield-per-recruit of 600 g when the instantaneous fishing mortality is 0.5 and recruitment ages are 4 to 6 years. Scamp spawned from April through August with a peak in May and June, and fed on fish, cephalopods, and crustaceans. The five most frequently occurring foods were unidentifiable fish, round scad (Decapterus punctatus), tomtate (Haemulon aurolineatum), unidentifiable serranids, and vermilion snapper (Rhomboplites aurorubens).

In this paper we estimate growth and mortality rates, present a yield-per-recruit model, and briefly discuss the reproductive cycle and diet of scamp, *Mycteroperca phenax* collected off North and South Carolina. There are no published research results on the growth, reproduction, or food habits of this species despite its wide distribution and importance to fisheries. Smith (1971) presented meristic and morphometric characteristics for scamp, as well as short ecological and distributional notes.

The scamp, a medium sized (to 25 kg) grouper (Serranidae, Epinephelinae) is found on subtropical reefs from Cape Hatteras, North Carolina south through the Gulf of Mexico (Randall, 1968; Smith, 1971). Occurring at depths from 40 to 100 m, the highly prized scamp is harvested by traps and trawls, and by both recreational and commercial hook and line methods. From 1973 to 1979, scamp contributed 34% of the total weight of grouper (348 mt) caught in the South Atlantic Bight headboat fishery.

MATERIALS AND METHODS

From 1972 to 1979, we obtained lengths (total, fork, or both) in millimeters and weights in grams of 3,075 scamp from the headboat catch (Huntsman, 1976) made between Cape Hatteras, North Carolina and Georgia. Fork lengths of 4,905 scamp from the commercial catch landed in South Carolina were recorded by personnel of the South Carolina Marine Resources Research Institute. Most fish (>95%) came from between Cape Lookout, North Carolina and Charleston, South Carolina and most

were landed from February through November. Life history materials obtained included otoliths (N = 703), gonads (N = 383), and stomachs (N = 326). Sampling occurred throughout the period and approximated randomness.

Scamp, like other groupers, are apparently protogynous hermaphrodites and sexing of many specimens is possible only after histological examination of the gonads. We knew the sex of only those individuals from which gonad samples were taken or whose gonads were well differentiated. Commercially caught fish are landed without viscera and cannot be sexed. The separation of growth curves (etc.) by sex for a protogynous species seems to us illogical because the sexes sequentially occur in the same body which has but a single growth curve and age and sex are confounded.

Because grouper scales are small, usually regenerated, and useless for age determinations, we used otoliths. Otoliths (sagittae) were exposed by cutting the skull transversely with a hacksaw or by scraping away the side of the otic capsule (Barans et al., 1979). The latter method is easily mastered and does not deface fish that might be mounted or sold. Whole otoliths are thick and opaque and must be cross-sectioned to expose growth rings. We used the sectioning apparatus and techniques described by Berry et al. (1977). The plane of sectioning included the focus and area anterior to the lateral (dorsal) projection (Moe, 1969). Left otoliths were used unless they were broken or illegible and right ones were substituted. Otolith sections were viewed in a darkened watch glass through a binocular microscope. Illumination by reflected, high-intensity light projected at a 45° angle revealed opaque and translucent (hyaline) rings, the opaque rings, which we hypothesized represented the end of one year's growth, were counted and the distances from the focus to the distal edge of each opaque ring and to the edge of the section were measured with an ocular micrometer (20× magnification, 1 ocular unit = 0.05 mm). For the most part only one reader viewed the otoliths, because the existence and location of the rings were usually unambiguous. In the few cases where two readers were needed agreement exceeded 90%. Rings suitable for age analysis occurred on 71.6% of the collected otoliths (total N = 703). The discarded otoliths, which evenly represented all fish sizes, were usually broken but a few lacked corresponding data on fish size or displayed unusual (probably pathological) calcification.

Using an otolith radius-fish length regression of the form FL = a + b(OR); where FL = fork length, OR = otolith radius, we back-calculated mean fish lengths at each age by substituting the means of the distances from the focus to each annulus for OR. The von Bertalanffy (1938) growth equation, $l_t = L_{\infty}(1 - e^{-K(t-t_{\omega})})$, was fitted to back-calculated length at age data by a non-linear, least squares method which made use of the Gauss-Newton algorithm (Dixon, 1981).

Mortality rates (Z) were estimated from catch curves (Everhart et al. 1975; Ricker, 1975). Regressions were fitted to the descending limb from the modal age plus one through all ages represented by at least one fish. The age-length key approach was used to obtain age frequencies for fish from which otoliths had not been taken. The otoliths from which ages were determined were from the same area and time period as the unaged fish. Fish of estimated age (N = 503) and of unknown age were grouped separately by 25 mm length intervals. The fish of unknown age were allocated to age groups by proportioning the unaged fish in each length interval according to the percentages of each age occurring in the corresponding length interval of aged fish.

Instantaneous natural mortality (M) was estimated by using the multiple regression of M on annual mean water temperature (°C) and on the von Bertalanffy parameters K and L_{∞} (Pauly, 1980–1981). Estimating M is a common and often insoluble problem. The Pauly method is suspect (Matheson and Huntsman, 1984) but lacking any other applicable nonarbitrary method we chose it. Fortunately, conclusions drawn from yield-per-recruit models, in which the estimated M is principally used, change little over the reasonable range of M estimates (Huntsman et al., 1983).

The fork length-total length relationship was expressed through a simple linear regression of untransformed data, but the curvilinear length-weight relationship was determined through a linear fit of data transformed to logarithms. The equation was then retransformed to the exponential form with the appropriate bias correction (Beauchamp and Olson, 1973).

We employed the Beverton and Holt (1957) yield-per-recruit model. The algorithm and notation follow Ricker (1975). Growth parameters were from the von Bertalanffy equation, and W^{∞} was estimated as the weight (based on the length-weight regression) corresponding to the asymptotic length. Growth was assumed to be isometric. Based on the existence of fish larger than those aged, maximum attainable age was estimated at 25 years. For this yield-per-recruit analysis the choice of maximum age is not critical because so few fish live to the maximum age.

Determining the status of the scamp fishery required estimates of F (annual instantaneous fishing mortality rate) and of t, (the age at recruitment). To estimate t, we determined, by inspection of length frequencies, the minimum length at which scamp became fully susceptible to the fishing gear. Based on the normal distribution, the probability that fish of each age would achieve the minimum length was estimated, and these probabilities were used to calculate a weighted mean age at recruitment (Huntsman et al., 1983).

Ovaries (N = 383) were examined macroscopically and assigned a stage of development: immature,

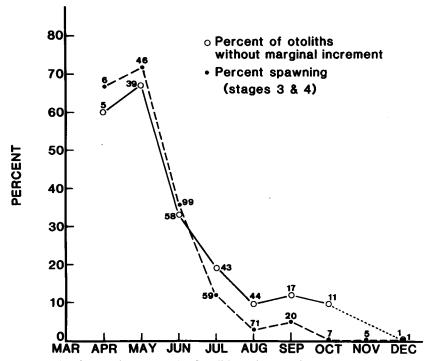


Figure 1. Relative frequencies by month of otolith sections lacking a marginal increment and of female scamp in spawning condition.

developing, visible eggs, and spawning (Manooch, 1975). Percentages of ovaries at each stage were calculated by month to determine the apparent spawning time.

Stomachs were removed from 326 fish in the field, placed in labeled cloth bags or cheese cloth, and preserved in a 4% solution of formaldehyde. In the laboratory, the volume of each stomach's contents was determined by displacement, the contents were separated, and the items were identified to the lowest possible taxon and counted. Empty stomachs were excluded. The data first were summarized in three ways: as percent frequency of occurrence (P; F, used by Pinkas et al., commonly and in this manuscript is the instantaneous fishing mortality rate); percent of total number (N); and percent of food volume (V). Frequency of occurrence of materials was the percentage of stomachs containing at least a portion of an item (taxon). Indices of relative importance (IRI) (Pinkas et al., 1971) were calculated as

$$IRI = (N + V)P.$$

RESULTS

Age and Growth.—Rings on otolith cross-sections were determined to be annuli by analyzing marginal increments (Fig. 1), by examining the frequencies of distances from the focus to the hypothesized annular rings (Fig. 2), and by satisfying the criteria of Van Oosten (1929) as follows. Otolith cross-section radii were directly proportional to and highly correlated with body length (Fig. 1) FL = -68.468 + 10.231(OR), $r^2 = 0.92$, N = 703 where FL = fork length (mm), and OR = otolith cross-section radius (mm). The number of rings increased with length, one mode occurred for each ring, and modes were consistently located for each annulus in progressively older fish (Fig. 2). Back-calculated lengths closely agreed with mean observed lengths at each age. The frequency of absence of a marginal increment (the distance between the opaque ring and cross-section edge) suggests that opaque rings formed once a year usually in April or May (Fig. 1).

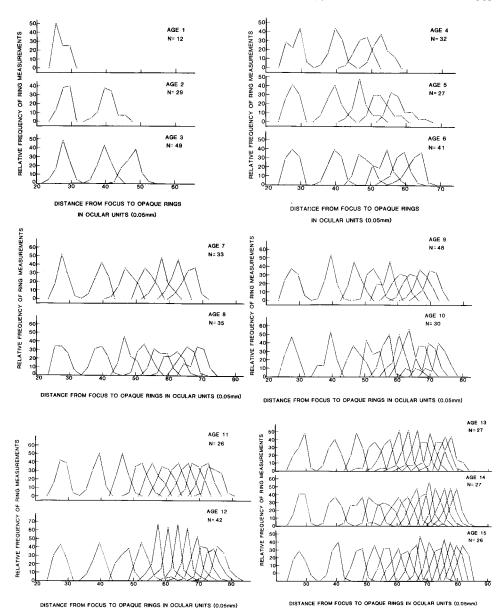


Figure 2. Relative frequency of distances from the focus to opaque rings on otoliths of scamp. Measurements are in ocular units (0.05 mm).

While there is a gap in the series of data on marginal increments (for midwinter when fishing was rare) the brevity of the gap in combination with the strong relationship of the reproductive cycle to that of marginal increments, and the fact that the congeneric gag Mycteroperca microlepis (Manooch and Haimovici, 1978) and every studied sympatric species (Manooch, 1982) forms annual rings, provides convincing evidence that only one ring forms annually. As recommended by Beamish and MacFarlane (1983) fish of advanced ages (≤ 10 years) as well as

	Num				Back-ca	alculated len	gth (FL mm	ı) at age					
Age	ber	1	2	3	4	5	6	7	8	9	10		
1	12	206.7											
2	29	220.0	346.9										
2 3	49	214.9	338.7	416.5									
4 5	32	218.0	340.8	415.4	468.7								
5	27	217.0	335.7	414.3	470.7	520.8							
6	41	214.9	339.7	423.6	482.0	529.0	572.0						
7	33	217.0	335.7	416.5	475.8	522.9	566.9	605.8					
8	35	213.9	332.6	414.3	469.7	518.8	559.7	598.6	632.4				
9	48	217.0	334.6	414.3	468.7	512.6	550.5	587.3	620.0	650.8			
10	30	212.9	333.6	414.3	465.6	508.6	548.5	583.2	617.0	647.7	678.4		
11	26	218.0	328.5	409.3	465.6	506.5	540.3	572.0	603.7	634.4	664.1		
12	42	212.9	333.6	416.5	471.7	514.7	549.5	581.2	610.9	640.5	667.1		
13	27	221.1	331.6	408.3	464.6	506.5	541.3	572.0	602.7	629.3	655.9		
14	27	221.1	334.6	410.3	466.6	506.5	543.3	574.0	602.7	627.2	652.8		
15	26	217.0	333.6	415.4	465.6	505.5	540.3	571.0	600.6	628.3	655.9		
16	9	207.8	330.5	413.4	467.6	513.7	547.4	577.1	604.7	628.3	650.8		
17	2	223.1	325.4	402.2	468.7	519.8	560.7	591.4	622.1	652.8	678.4		
18	4	216.0	345.9	417.5	473.8	512.6	545.4	576.1	606.8	632.4	655.9		
19	1	197.5	340.8	432.8	494.2	545.5	576.1	608.8	637.5	668.1	698.8		
20	2	212.9	340.8	417.5	473.8	519.8	571.0	601.7	637.5	673.3	698.8		
21	1	228.2	340.8	432.8	494.2	535.2	565.8	596.5	627.2	647.7	668.1		
No.	cal-												
cu	lations	503	491	462	413	381	354	313	280	245	197		
Weig	ghted												
me	eans	216.1	335.9	415.0	470.3	514.8	552.5	584.0	612.8	638.7	663.1		
SE (mean)	3.3	4.3	3.9	5.2	7.7	10.7	11.4	10.6	9.9	8.2		
Incre	ement	216.1	119.8	79.1	55.3	44.5	37.7	31.5	28.8	25.9	24.4		

Table 1. Back-calculated lengths of 503 scamp aged by reading sectioned otoliths

young fish were included in the marginal increment analysis and other age validation procedures.

Scamp are long-lived (to >21 years) and attain their maximum size slowly (Table 1). The von Bertalanffy equation is: $l_t = 985(1 - e^{-0.092(t+2.45)})$ where $l_t =$ fork length in millimeters at year t.

Observed, back-calculated, and modeled growth curves agree closely (Fig. 3). Observed mean lengths were larger than back-calculated lengths probably because of growth between times of annulus formation and capture.

Morphometric Relationships.—Because the long exsertions on the caudal fin often appeared worn or broken, we feared that total length (our usual measure) was unacceptably imprecise. Consequently in 1975 we began recording both total and fork lengths, believing the latter to be more useful. The relationship used to convert pre-1975 measurements of TL to FL is

$$FL = 0.870(TL) + 23.625$$
, $N = 33$, $r^2 = 0.98$.

The overall equation describing the relationship of weight to length is $W = 2.46 \times 10^{-8} (FL)^{2.913}$, N = 693, $r^2 = 0.98$. Scamp measuring 200, 400, 600, 800, and 1,000 mm FL would be estimated to weigh 0.12, 0.93, 3.05, 7.04, and 13.49 kg.

Mortality Estimates.—Determining mortality rates from the peculiarly shaped catch curves (Fig. 4) of scamp is troubling. For undetermined reasons (possibilities

Table 1. Continued

					ated length (FL mm) at a	ge			· · · · · · · · · · · · · · · · · · ·
11	12	13	14	15	16	17	18	19	20	21

691.7										
692.7	715.2									
681.5	704.0	725.4								
678.4	700.9	722.4	742.8							
680.4	702.9	725.4	746.9	768.4						
674.3	695.8	717.3	737.7	759.2	774.7					
698.8	719.3	739.8	760.2	780.7	801.2	821.6				
676.3	696.8	724.4	741.8	762.3	789.7	801.2	811.4			
719.3	739.8	770.5	790.9	811.4	831.9	852.3	872.8	893.2		
719.3	739.8	765.4	789.7	801.2	821.6	837.0	852.3	867.7	883.0	
698.8	719.3	739.8	760.2	780.7	801.2	821.6	842.1	862.6	883.0	893.2
167	141	99	72	45	19	10	8	4	3	1
685.7	706.9	725.5	746.0	769.2	790.5	819.6	833.1	872.8	883.0	893.2
8.3	8.3	9.2	11.0	17.4	18.4	24.7	13.8	0.0	0.0	0.0
22.6	21.2	18.6	20.6	23.2	21.3	29.1	13.5	39.7	10.2	10.2

include irregular and delayed recruitment to the gear, immigration, sampling bias, and overestimates of fish ages), several ages are almost equally frequent, and a clear downward trend in the catch curve does not appear until age 9 or greater. Catch curves for the congeneric gag (*Mycteroperca microlepis*) from the same area, habitat, and fishery are similarly puzzling (Manooch and Haimovici, 1978). However, those of the closely related snowy grouper (*Epinephelus niveatus*) and speckled hind (*E. drummondhayi*) (Matheson, 1981) from the same fishery have a distinct mode as do catch curves for gag from the west coast of Florida¹.

Point estimates of the instantaneous total mortality rate (Z), based on frequencies of fish 13 years and older, from the headboat fishery for the years 1972 to 1979 were 0.52, 0.59, 0.44, 0.64, 0.66, 0.48, 0.44, and 0.29. Estimates based on samples from the commercial hook and line fishery from 1976 to 1979 were 0.91, 0.57, 0.79, and 0.61. The small number of ages greater than 13 years available for the regression analyses of catch curves limited the power of tests for differences between years and fisheries. Nonetheless, an analysis of covariance revealed that the mean rate for all years determined from samples from the commercial fishery (Z = 0.63) was significantly different from that in the recreational fishery (Z = 0.47, P < 0.05). Within fisheries, differences between years could not be discerned. If K = 0.09, $L_{\infty} = 98.5$ cm, and mean water temperature = 17°C (based on

¹ Schlieder, R. Age, growth and reproduction of the gag grouper, Mycteroperca microlepis, from the eastern Gulf of Mexico. Unpublished ms.

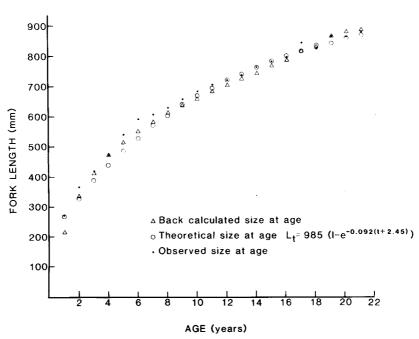


Figure 3. Observed, theoretical, and back-calculated lengths at ages 1 to 21 of scamp.

field observations and sea surface temperatures (U.S. National Oceanic and Atmospheric Administration, 1973), M = 0.21.

Age at Recruitment.—Average ages of recruitment to the fishery (t_r) as estimated by the weighted mean ages at first capture were, for the recreational fishery, 5.4 years from 1972 to 1975, and 3.1 years from 1977 to 1979, and for the commercial fishery, 4.0 years from 1976 to 1979.

Yield-Per-Recruit. — The yield/recruit (Y/R) model (Fig. 5) for scamp is much like that for other reef fishes from the South Atlantic Bight (Huntsman et al., 1983). Almost all of the maximum Y/R (~ 600 g) can be attained at F (instantaneous fishing mortality) of 0.3 or less (Y/R at F = 0.3 and t_r = 5 years is 592 g, 94% of the maximum). A moderately great recruitment age (4 years) is required to produce maximum Y/R if F exceeds 0.5, but if F is slightly less, an age of 3 or less will allow almost all the yield available to be taken.

Status of the Fishery. —From 1972 to 1975, scamp were recruited to the headboat fishery at a mean age of 5.4 years and from 1977 to 1979 at 3.1 years. F (=Z — M) was about 0.26 from 1972 to 1979. Under these conditions about 85% of the potential maximum Y/R was taken. On the commercial fishing grounds (which are larger than and include the headboat grounds), F was 0.42 and recruitment age was 4.0 years. These conditions should have allowed taking 94% of the available Y/R.

Spawning.—Ovaries in the final two stages of development (visible eggs and spawning) occurred from April through August (Fig. 1 and Table 2). The highest relative frequency of these stages was in May and June, suggesting that spawning peaked then. Scamp off the west coast of Florida spawn slightly earlier, March through May (M. Godcharles, pers. comm.). Ovaries at spawning stage were greatly

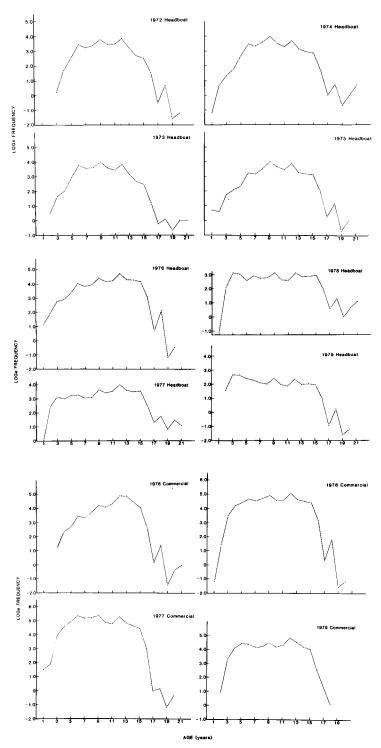


Figure 4. Catch curves of scamp sampled from the headboat fishery off North Carolina and South Carolina (1972–1979) and from the commercial catch landed in South Carolina (1976–1979).

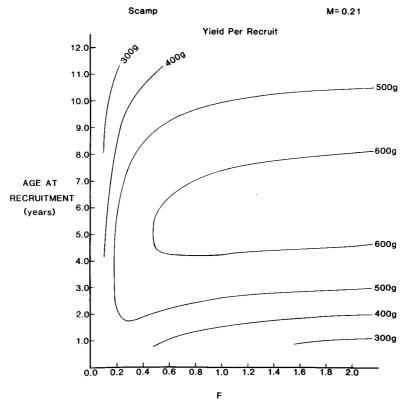


Figure 5. A Beverton and Holt yield-per-recruit model for scamp with M = 0.21.

enlarged, pale yellow, and contained eggs about 1 mm in diameter. Water temperatures at the bottom (30 to 61 m) during May and June ranged from approximately 22 to 25°C (R. O. Parker, pers. comm.).

Foods.—Of the 326 stomachs examined, only 91 (27.9%) contained food. Empty stomachs frequently resulted from forced voiding during capture as internal gases expanded during the fish's ascent to the surface.

Of three groups of foods, fish, cephalopods, and crustaceans constituting the diet, fish were most important (Table 3). Unidentifiable fish remains, round scad (Decapterus punctatus), tomtate (Haemulon aurolineatum), unidentifiable serranids and vermilion snapper (Rhomboplites aurorubens), had the highest IRI values (Table 3). Invertebrates (seven groups) were present but unimportant. Most prey lived on or near the bottom. Gag collected off Florida's west coast also fed predominantly on bottom-dwelling fishes and crustaceans (C. Saloman, pers. comm.).

DISCUSSION

Scamp attain their maximum size slowly (K = 0.092) and have a long life span (>21 years). This growth pattern is shared not only by numerous other groupers (for which K ranges from 0.06 to 0.18 and maximum age from 13 to 28 years) (Manooch and Haimovici, 1978; Muhlia Melo, 1975; Moe, 1969; Nagelkerken, 1979; Burnett-Herkes, 1975; Olsen and LaPlace, 1978; Matheson, 1981; Moore and Labisky, 1984), but also by South Atlantic Bight reef fishes of other families

Table 2. Relative frequency of gonad stages by month of collection

		Gonad stage*										
	Total .	1		2		3		4				
Month	No.	No.	%	No.	%	No.	%	No.	%			
March	1	_	_	1	100.0							
April	6	_	_	2	33.3	2	33.3	2	33.3			
May	46	_	_	13	28.3	11	23.9	22	47.8			
June	99	5	5.0	59	59.6	15	15.2	20	20.2			
July	59	4	6.7	48	81.4	5	8.5	2	3.4			
August	71	2	2.8	67	94.4	1	1.4	1	1.4			
September	20	_	_	19	95.0	1	5.0	_	_			
October	7	1	14.3	6	85.7	_	_	_	_			
November	5	_		5	100.0	_	_	_	_			
December	1	_	_	1	100.0	_	_	_	_			

^{*} Stage 1—undeveloped, Stage 2—developing, Stage 3—visible eggs, Stage 4—clear eggs.

whose K's range from 0.10 to 0.22 and maximum ages from 9 to 16 years (Manooch and Huntsman, 1977; Grimes, 1978; Nelson and Manooch, 1982; Manooch, 1978; Waltz et al., 1982; Mercer, 1978; Cupka et al., 1973; Horvath and Grimes²; Manooch and Barans, 1982). The generality of low K and long life among live bottom reef fishes suggests that these traits are related to evolutionary success in the reef environment of the South Atlantic Bight (Huntsman, 1981). A probable

Table 3. Index of relative importance values for foods found in the scamp stomachs

Item	IRI value
Unidentified fish	2,269.0
Synodus sp.	0.7
Unidentified synodontid	1.1
Porichthys plectrodon	2.2
Holocentridae	2.2
Centropristis ocyurus	5.2
Centropristis striata	3.0
Centropristis sp.	22.3
Unidentified serranid	80.2
Priacanthus arenatus	2.1
Decapterus punctatus	1,077.0
Unidentified carangid	10.1
Rhomboplites aurorubens	37.1
Haemulon aurolineatum	220.0
Stenotomus sp.	4.8
Unidentified sparid	1.7
Sciaenidae	1.7
Chromis sp.	6.0
Labridae	1.1
Bothidae	0.8
Octopus sp.	0.8
Metapenaeopsis goodei	9.5
Penaeidae	3.6
Solenocera sp.	2.5
Unidentified Natantia	2.3
Ovalipea sp.	1.4
Portunus sp.	0.6

² Horvath, M. and C. B. Grimes. Age and growth of the knobbed porgy from the South Atlantic Bight. Unpublished ms:

benefit is that long life and relatively great body size maximize gamete and zygote production and enable reef fishes to overcome the apparently low probability of the pelagic offspring encountering favorable habitat. A concurrent result of the pattern is that near maximal yields of the scamp and associated reef species can be taken with fisheries of low intensity. Indeed even if F is as low as 0.2, about 80% of the maximal yield-per-recruit of scamp can be taken over a wide range of recruitment ages.

We were surprised that Z calculated from the headboat catches was less than that calculated from the commercial catch, because the commercial fishery operates over a large area that includes the headboat grounds. For speckled hind and snowy grouper, mortality rates were higher in the headboat fishery, suggesting that the elevated Z resulted from the concurrence of commercial and recreational effort on the headboat grounds (Matheson and Huntsman, 1984). We can offer no reasonable hypothesis to explain the estimated mortality rates of scamp.

A more precise understanding of scamp population dynamics will not occur until we determine the cause of the unusual distributions of age frequency. Precise estimation of mortality rates from the available catch curves is very difficult and may require one or more of the following: (1) More precise specification of geographic source of samples from the fisheries, (2) Tagging to allow description of movements, (3) Fishery-independent sampling to provide a better measure of abundance of younger fish, (4) Increased numbers of fish aged by otoliths so that the numbers of old fish in samples are increased and a better age-length key can be established and (5) Larger samples for length frequencies.

The scamp is perhaps our most prized grouper around the continental United States. Describing the population parameters of this species is of great importance to reef fishery management efforts currently underway in the southeastern United States.

ACKNOWLEDGMENTS

We thank G. Ulrich of the South Carolina Marine Resources Research Institute who allowed us to use the information on landings of groupers in South Carolina. R. Dixon and numerous temporary samplers collected biological materials from headboat catches. A. Chester, W. Nicholson, J. Merriner, and R. Nelson reviewed the manuscript.

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DATE ACCEPTED: December 19, 1984.

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